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GENETIC ANALYSIS FOR EARLINESS AND YIELD TRAITS IN MAIZE

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Abstract

Five white kernel maize inbred lines with distinct genetic make-up were crossed in a 5 × 5 complete diallel fashion during spring season 2011 at Cereal Crops Research Institute (CCRI), Pirsabak - Nowshera, Pakistan. The resulting 20 F_1 hybrids, their five inbred lines and two checks hybrids (OPV 'Jalal' and 'Pioneer hybrid 30K08') were further evaluated during subsequent summer season 2011 at four locations. Present research was designed to study the genetic mechanisms controlling various earliness and yield traits through Hayman's diallel approach. Genotypes, locations and genotype by environment interactions (GEI) showed significant ($p \leq 0.01$) differences for all the traits studied. Significant genotypic differences for various traits justified to carryout the Hayman's genetic analysis. For adequacy, the additive-dominance model was adequate / partially adequate for various traits at all the locations. According to genetic analysis, the key components of genetic variances i.e., additive (D) and dominance components (H1, H2) and average degree of dominance revealed that dominance components were predominant and overdominance type of gene action played an important role in the inheritance of all the traits at different locations. Genetic analysis further revealed unequal proportion of positive (U) and negative (V) alleles in the loci (H2<H1) with asymmetrical distribution of genes in the parental genotypes (H2/4H1 < 0.25) for majority of the traits. Broad sense heritability values were higher for days to 50% tasseling (0.89 to 0.97), days to 50% silking (0.91 to 0.97), ear length (0.86 to 0.99), 1000-grain weight (0.92 to 0.97) and grain yield (0.98 to 0.99), respectively at all the locations. Narrow sense heritability for above traits was low to medium ranging from 0.12 to 0.23, 0.17 to 0.33, 0.13 to 0.36, 0.10 to 0.51 and 0.07 to 0.11, respectively at all the locations. Desirable high genetic gain values were observed for yield traits while for earliness the values were moderate. Due to non-additive genes controlling various traits and high broad sense heritability estimates, the promising F_1 hybrids could be developed in future breeding programs for production of early maturing and high yielding maize hybrids and cultivars through selection from later segregating generations.

Key words: Diallel crosses, Additive dominance model, Components of genetic variances, Broad and narrow sense heritability, Genetic gain, *Zea mays* L.

Introduction

Maize (*Zea mays* L.) is an important cereal crop of the world grown in irrigated and rain-fed areas, and ranks third after wheat and rice (Gerpacio & Pingali, 2007). It is an annual short day plant and belongs to family poaceae and tribe Maydeae. Maize utilizes solar radiations more efficiently than other cereals. It is grown at an altitude of 3300 meters above sea level and from 50^0 N to 40^0S latitude in temperate, sub-tropical and tropical regions of the world (Iqbal, 2009; Sajjad *et al*., 2016). Maize plant is monoecious and protandrous, and hot dry weather usually accelerates pollen shedding (Poehlman, 1977). It can be grown on all types of soils ranging from sandy loam to clay loam. However, medium texture soil of pH 6.5 to 7.5 is the most suitable for its successful cultivation.

In Pakistan, maize is third important cereal crop after wheat and rice (Hussain *et al*., 2011). Maize is cultivated as multipurpose crop for food, feed and fodder by the farming community, who largely lives in rural areas. The use of maize in Pakistan as direct human food is decreasing; however its industrial use is increasing at a much faster rate. In Pakistan, maize was grown on an area of 1.334 million hectares and total production was 6.13 million tones with average grain yield of 4.595 tons ha^{-1} (PBS, 2016-17).

In Khyber Pakhtunkhwa province of Pakistan, after wheat, the maize is the second important summer cereal with an area of 0.448 million hectares and production of 0.849 million tons with average grain yield of 1.896 tons ha^{-1} (BS-PDP, 2015-16). In Khyber Pakhtunkhwa, more than 27% of the total cultivated area is occupied by maize, with total cropped area of 42% (Iqbal *et al*., 2010). In the mountainous areas of Khyber Pakhtunkhwa, maize is utilized as an important staple food by the farming community as well as source of green and dry fodder for livestock (Iqbal *et al*., 2010; Khan *et al*., 2011).

Production and evolution of high yielding and well-adopted cultivars with desirable characters is a continuous process and needs to understand in detail the genetic mechanism controlling yield and yield contributing traits (Saleem *et al*., 2002). Large numbers of breeding procedures have been developed to increase the economic yield of different maize populations and their hybrids. In order to select the prominent specific cross combination as hybrid, large number of selected inbred lines are crossed (Unay *et al*., 2004). Before starting the breeding program for the development of promising maize hybrids/cultivars, it is of utmost importance to assess the germplasm for earliness, morphological, and yield traits, and to study their genetic architecture, because exploitation of genetic variability in the germplasm of any crop species is considered the key point for making further genetic improvement in economically important traits. In maize, greater magnitude of genetic variability has been reported which indicates the potential for genetic improvement (Wattoo *et al*., 2009). To tailor a plant genotype with desirable combination of traits, comprehensive information

regarding genetic mechanisms controlling various variables as well as association of various traits with yield is considered a pre-requisite to launch a well designed breeding program.

Conventional breeding has sustainable base in the present era of molecular breeding. It is well known fact that application of molecular markers must be certified through conventional breeding (Ali, 2015; Ali *et al*., 2017; Sajjad *et al*., 2016). Transgressive segregation depends upon categorizing the genotypes having potential of transmitting desirable traits in specific genotypic combinations. Diallel analysis and additive dominance models are the established mechanisms of conventional breeding to utilize allelic and non-allelic gene actions, nature and magnitude of genetic variances in specific combinations. Gene action is described in statistical terms as additive, dominant and epistatic and their interactions with environmental factors (Zia & Chaudhry, 1980; Ismail, 1996; Shabbir & Saleem, 2002; Wattoo *et al.*, 2009).

Genetic analysis work is dependable and effective technique for identification of superior genotypes, and the gene action involved in management of various attributes (Zia & Chaudhry, 1980). To introduce genetic variability, diallel cross analysis and mutation have been widely utilized by the plant breeders (Hayman, 1954a, b; Jinks, 1954; Saeed & Saleem, 2000; Ali *et al*., 2007). Consequently, the use of genotypes with desirable components of genetic variance is a continuous pre-requisite for synthesis of physiologically efficient and genetically superior genotypes showing promise for increased production per unit area under a given set of environments. All such endeavors need some genetic information and knowledge about the type of gene action involved in various agronomic and quality traits. Therefore, in light of these considerations, the present research was designed with the objectives to study the genetic mechanism of various plant characters through Hayman's approach in 5 × 5 complete diallel crosses of maize.

Materials and Methods

Breeding material and procedure: Five white kernel maize inbred lines with distinct genetic make-up were crossed in a complete diallel fashion during spring crop season 2011 at Cereal Crops Research Institute (CCRI), Pirsabak - Nowshera, Khyber Pakhtunkhwa, Pakistan (Table 1). The resulting 20 F_1 hybrids, their five parental inbred lines and two check hybrids (OPV 'Jalal' and 'Pioneer hybrid 30K08') were further evaluated during subsequent summer crop season 2011. The field experiments were carried-out at four different locations (environments will be used interchangeably) i.e., a) Cereal Crops Research Institute (CCRI), Pirsabak - Nowshera, b) Agricultural Research Institute (North) Mingora - Swat, c) Agricultural Research Station, Baffa - Mansehra, and d) University of Haripur, Haripur - Khyber Pakhtunkhwa, Pakistan. All the experiments at four different locations were laid-out in a randomized complete block design with three replications. Experimental sub-plots comprised of four each rows for all entries. Rows and plants spacing were kept 75 and 25 cm, respectively with five meters length in all the experiments. Recommended cultural practices and inputs were uniformly applied to all the genotypes at all the locations.

Measurement of traits: Ten plants were randomly selected and used for recording of the data of each trait in each treatment/replication/location, and data were recorded on the following five variables. Data regarding days to 50% tasseling and silking were recorded by regular visits to the field and days were counted from sowing to the day when 50% of the plants produced tassels and silks in a genotype in each subplot (Hinze & Lamkey, 2003; Khan *et al*., 2004). Average ear length was measured. Random sample of 1000 grains were taken from final produce of each entry and their weight was recorded in grams using electric balance. Grain yield (kg ha^{-1}) of each genotype was calculated after harvesting and adjusting fresh ear weight to 150 g kg^{-1} grain moisture by using following relationship (Carangal *et al*., 1971).

$$Grain\ yield\ (kg\ ha^{-1}) = \frac{(100 - MC) \times FEW \times Shelling\ coefficient \times 10{,}000}{(100 - 15) \times Plot\ area}$$

where;
MC = Moisture content (%) in grains at harvest
FEW = Fresh ear weight (kg) at harvest
Shelling coefficient = Shelling percentage / 100

Table 1. Pedigree of maize parental inbred lines and their F_1 diallel hybrids.

Parental inbred lines	Pedigree
FRHW-22(F2)-5	Male parental single cross of Babar
FRHW-22(F2)-4-7	Male parental single cross of Babar
FRHW-20-4	Female parental single cross of Babar
PSEV3-120-2-2-2	Derived from white maize population PSEV-3 (base population of commercial 'OPV Jalal')
SW-6-6-3-6	Derived from open pollinated long duration variety Sarhad White

F_1 Crosses	F_1 Crosses
FRHW-22 (F2)-5 × FRHW-22 (F2)-4-7	FRHW-20-4 × PSEV3-120-2-2-2
FRHW-22 (F2)-5 × FRHW-20-4	FRHW-20-4 × SW-6-6-3-6
FRHW-22 (F2)-5 × PSEV3-120-2-2-2	PSEV3-120-2-2-2 × FRHW-22 (F2)-5
FRHW-22 (F2)-5 × SW-6-6-3-6	PSEV3-120-2-2-2 × FRHW-22 (F2)-4-7
FRHW-22 (F2)-4-7 × FRHW-22 (F2)-5	PSEV3-120-2-2-2 × FRHW-20-4
FRHW-22 (F2)-4-7 × FRHW-20-4	PSEV3-120-2-2-2 × SW-6-6-3-6
FRHW-22 (F2)-4-7 × PSEV3-120-2-2-2	SW-6-6-3-6 × FRHW-22 (F2)-5
FRHW-22 (F2)-4-7 × SW-6-6-3-6	SW-6-6-3-6 × FRHW-22 (F2)-4-7
FRHW-20-4 × FRHW-22 (F2)-5	SW-6-6-3-6 × FRHW-20-4
FRHW-20-4 × FRHW-22 (F2)-4-7	SW-6-6-3-6 × PSEV3-120-2-2-2

Statistical analyses

Genotype by environment interaction analysis was carried out according to Gomez &Gomez (1984). Hayman's diallel approach (1954a, b) and Mather's concept of D, H components of genetic variation for additive and dominance variances, respectively (D is used for additive variance instead of A, and H_1 and H_2 for dominance components of genetic variance instead of D) were used to study the genetic effects for various traits at all the locations. Mather and Jinks (1982) have also made the recent development about this technique and components of genetic variation were estimated by adopting that method of diallel analysis (Singh & Chaudhary, 1985).Genetic gain from selection for a trait in a cross under 10% selection intensity (1.755) and genetic gain as a percent of the sample mean were computed for each trait in F_1 generation (Breese, 1972).

Results and Discussion

Success of maize breeding programme is predominantly based on the choice and use of promising parental inbred lines for hybridization, followed by selection for favourable gene combinations in homozygous lines under diverse environments. Therefore, information regarding genetic variability and genetic analysis provides dependable tools to the breeder for crop improvement. Breeding programmes in various crops have categorically established that the *per se* production performance of genotypes do not provide dependable basis for their productivity in cross combinations. Thus crossing in a diallel fashion is an effective technique for identification of superior genotypes. To achieve these objectives, comprehensive studies of the genetic mechanism for the control of various traits in hybrid populations under different environmental conditions have been advocated in various crop species (Hayman, 1954a, b; Mather & Jinks, 1982). In present study, genotypes, locations and genotype by environment interactions (GEI) showed significant ($p \leq 0.01$) differences for all the traits (Table 2). Significant genotypic differences for various traits justified to carryout the genetic analysis.

Genetic Analysis

Adequacy of additive-dominance model: In order to test the adequacy of the additive-dominance model and validity of diallel assumptions underlying the genetic model for data sets of various traits, were tested through three scaling tests i.e., t^2 test, regression analysis and arrays analysis of variance (Wr ± Vr and Wr – Vr) (Table 3). According to Mather &Jinks (1982), the regression coefficient is expected to be significantly different from zero (b = 0) but not from unity (b = 1). Significant differences between the arrays (Wr ± Vr) and non-significant differences within the arrays (Wr – Vr) show the presence of dominance and absence of epistasis (Mather & Jinks, 1982). Non-significant value of t^2 test also confirms absence of non-allelic interaction and therefore, the genes will be independent in their action for random association. If all the tests are found in favor of assumptions, the genetic model is declared fully adequate, while if at least one test fulfills the assumptions then it is quoted as partially adequate. Failure of all the three tests completely invalidates the additive-dominance model.

According to adequacy of additive-dominance model, the model was partially adequate for days to 50% tasseling and silking, 1000-grain weight, and grain yield, while inadequate for ear length at CCRI (Table 3). At Haripur, the additive dominance model was fully adequate for 1000-grain weight while partially suitable for other four traits. In Mansehra, the data sets of the traits revealed full adequacy for days to 50% tasseling and 1000-grain weight and partial adequacy for other three traits. At fourth location i.e., Swat, the additive dominance model was fully adequate for all the traits except ear length which showed partially adequacy.

Components of genetic variation for various traits: Components of genetic variance for various traits in F_1 generation are discussed here under.

Days to 50% tasseling: At CCRI, both additive and dominance components were significant which indicated importance of additive as well as dominant gene effects for days to 50% tasseling in F_1 generation (Table 4). However, the values of H_1 and H_2 were greater than D, indicating non-additive type of gene action controlling the character as also confirmed by average degree of dominance i.e., $H_1/D^{1/2}$ (1.53). Positive value of F showed that dominant genes were more important than recessive. Significant value of h^2 pointed out the dominant genes due to heterozygous loci, which is also supported by the value of $4DH_1^{½} \pm F/4DH_1^{1/2} – F$ (2.10). Unequal values of H_1 and H_2 components and the ratio of $H_2/4H_1$ (0.21) exhibited the irregular distribution of positive and negative genes among the parental inbred lines. Broad sense heritability (0.96) was higher than narrow sense heritability (0.23) indicating less contribution of additive genetic variation for days to 50% tasseling in F_1 populations at CCRI. Genetic gain and its value as percent of population mean were 4.15 days and 7.99%, respectively.

Components of genetic variance showed significant additive and dominance values, while F, h^2 and E were non-significant for days to 50% tasseling in F_1 generation at Haripur (Table 4). These results revealed that the said trait was advocated by both additive and dominance gene effects. However, the magnitude of dominance variation was greater than additive which is also authenticated by the ratio of $H_1/D^{1/2}$ (1.53) and $4DH_1^{½} \pm F/4DH_1^{1/2} – F$ (2.43). Positive value of F indicated that dominant genes were more frequent than recessive. The value of H_1 was greater than H_2 indicating that the positive and negative genes were unequally distributed between parental genotypes which also supported by the ratio of $H_2/4H_1$ (0.20). Broad sense heritability (0.97) was greater than narrow sense (0.25) revealing greater contribution of non-additive inheritance for days to 50% tasseling in F_1 populations at Haripur. Genetic gain and its value as percent of population mean were 4.19 days and 8.08%, respectively for days to 50% tasseling.

Table 2. Mean squares for various traits in 5 × 5 F_1 diallel cross of maize evaluated at four locations.

Variables	Locations	Reps with in location	Genotypes	G × L	Error	CV (%)
Days to 50% tasseling	693.765**	1.475**	18.205**	7.289**	0.469	1.32
Days to 50% silking	621.789**	2.917**	17.983**	7.806**	0.458	1.19
Ear length	222.264**	3.740**	59.879**	3.455**	0.496	4.29
1000-grain weight	0.20166**	0.00155*	0.03745**	0.00328**	0.00071	8.57
Grain yield	2.303E±08**	329509 ns	5.750E±07**	3591133**	179730	4.68

Table 3. Adequacy of additive-dominance model for various traits in 5 × 5 F_1 diallel cross of maize at four locations.

Traits	t^2 test	Regression analysis		ANOVA of arrays		Conclusions
		b_0	b_1	Wr ± Vr	Wr - Vr	
CCRI						
Days to 50% tasseling	0.02 ns	0.07 ns	1.53ns	6.44 **	41.79 **	Partially adequate
Days to 50% silking	0.39 ns	1.19 ns	1.63ns	6.76 **	14.8 **	Partially adequate
Ear length	48.46**	17.25**	8.39**	1615.65**	32.51**	Inadequate
1000-grain weight	1.19ns	4.82*	1.51ns	25.54**	4.41*	Partially adequate
Grain yield	1.83ns	1.36ns	2.58ns	26.22**	13.87**	Partially adequate
Haripur						
Days to 50% tasseling	0.004 ns	2.21 ns	0.54 ns	141.18**	23.21**	Partially Adequate
Days to 50% silking	0.004 ns	2.19 ns	0.67 ns	34.49**	15.71**	Partially Adequate
Ear length	1.29ns	5.09*	1.54ns	6.27**	4.89*	Partially adequate
1000-grain weight	0.09 ns	3.58*	0.11 ns	7.21**	1.88 ns	Adequate
Grain yield	1.65ns	11.75**	1.48ns	299.46**	21.85**	Partially adequate
Mansehra						
Days to 50% tasseling	0.01ns	4.83*	0.4ns	22.26**	1.59ns	Adequate
Days to 50% silking	0.17ns	2.88ns	0.2ns	112.32**	13.19**	Partially adequate
Ear length	2.47ns	9.52 **	11.86ns	7.95 **	2.78 ns	Partially adequate
1000-grain weight	4.03ns	14.74 **	2.24ns	15.03 **	0.67 ns	Adequate
Grain yield	1.47 ns	1.08 ns	2.51 ns	29.13**	17.73**	Partially adequate
Swat						
Days to 50% tasseling	0.01ns	4.83*	0.4ns	22.26**	1.59ns	Adequate
Days to 50% silking	0.18ns	4.53*	0.76ns	15.99**	1.37ns	Adequate
Ear length	1.06ns	4.93 *	1.43ns	11.28 **	6.47 **	Partially Adequate
1000-grain weight	0.95ns	8.12 **	1.22ns	7.77 **	0.73 ns	Adequate
Grain yield	1.33 ns	7.80**	1.43 ns	21.76**	2.01 ns	Adequate

Genetic components of variance revealed that additive (D), dominance (H_1, H_2, h^2) and covariance of additive and dominance effects (F) were significant for days to 50% tasseling in F_1 generation at Mansehra (Table 4). Environmental variation (E) was non-significant and having no influence in the inheritance of said trait. Both additive and dominant type of gene actions were involved in inheritance of said trait. However, dominance components (H_1, H_2) were greater than D and the average degree of dominance (1.51) was more than unity, confirming a high level of dominance affecting this trait. Significance of F revealed that dominant genes were in excess than recessive and that is also verified by the ratio of $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (2.05), and h^2 confirmed the unidirectional dominance. The dominance component H_1 was greater than H_2, indicating asymmetrical distribution of positive and negative genes in parental genotypes as confirmed by the ratio of $H_2/4H_1$ (0.23) which was deviated from 0.25. Broad sense (0.89) heritability was high than narrow sense (0.12) heritability, indicating that most of the genetic variation was contributed by non-additive genes for days to 50% tasseling in F_1 generation at Mansehra. Genetic gain was 3.85 days while its value as percent of population mean was 7.41%.

In Swat, components of genetic variance such as D (4.21), H_1 (9.58), H_2 (8.76), F (4.38) and h^2 (7.51) were significant indicating presence of both additive and dominant type of gene actions for days to 50% tasseling in F_1 hybrids (Table 4). However, magnitude of dominant gene effects was greater than additive as revealed by average degree of dominance i.e., $H_1/D^{1/2}$ (1.51). The value of dominance component H_1 was greater thanH_2, and the ratio of $H_2/4H_1$ (0.23) was less than 0.25 showing unequal frequencies of positive and negative genes. Significant value of F showed dominant alleles in the parental genotypes is also supported by the ratio of $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (2.43), and dominance was unidirectional as verified by significant value of h^2. High broad (0.90) and low narrow sense (0.12) heritabilities were observed for said trait which revealed that most of the genetic variation was contributed by dominant genes for days to 50% tasseling at Swat. Genetic gain and its value as percent of population mean were 4.02 days and 7.74%, respectively for days to 50% tasseling in F_1 generation at Swat.

Table 4. Components of genetic variance for days to 50% tasseling and silking in 5 × 5 F_1 diallel cross of maize.

Components of genetic variance	Days to 50% tasseling				Days to 50% silking			
	CCRI	Haripur	Mansehra	Swat	CCRI	Haripur	Mansehra	Swat
D	5.88 ± 1.68*	4.79 ± 1.3*1	4.21 ± 0.67*	3.82 ± 0.78*	7.23 ± 1.68*	3.58 ± 0.77*	3.56 ± 1.27*	4.23 ± 0.57*
H_1	13.70 ± 4.53*	9.41 ± 3.53*	9.58 ± 1.82*	11.84 ± 2.09*	12.29 ± 4.55*	8.02 ± 2.07*	12.62 ± 3.42*	8.93 ± 1.55*
H_2	11.48 ± 4.11*	7.36 ± 3.20*	8.76 ± 1.65*	9.06 ± 1.90*	10.83 ± 4.12*	7.34 ± 1.88*	10.03 ± 3.10*	7.96 ± 1.40*
F	6.36 ± 4.19	5.60 ± 3.26	4.38 ± 1.68*	5.61 ± 1.94*	6.71 ± 4.21	2.41 ± 1.91	4.55 ± 3.16	4.29 ± 1.43*
h^2	10.85 ± 2.78*	0.09 ± 2.16	7.51 ± 1.11*	7.70 ± 1.28*	10.47 ± 2.78*	-0.05 ± 1.27	5.34 ± 2.10*	7.54 ± 0.95*
E	0.14 ± 0.69	0.07 ± 0.53	0.29 ±0.27	0.22 ± 0.32	0.19 ± 0.69	0.08 ± 0.31	0.25 ± 0.52	0.24 ± 0.23
$(H_1/D)^{1/2}$	1.53	1.40	1.51	1.76	1.30	1.50	1.88	1.45
$H_2/4H_1$	0.21	0.20	0.23	0.19	0.22	0.23	0.20	0.22
KD / KR	2.10	2.43	2.05	2.43	2.11	1.58	2.03	2.07
h^2/H_2	0.94	0.01	0.86	0.85	0.97	-0.01	0.53	0.95
Heritability (ns)	0.23	0.25	0.12	0.17	0.25	0.33	0.23	0.17
Heritability (bs)	0.96	0.97	0.89	0.93	0.95	0.97	0.93	0.91
Genetic gain	4.15	4.19	3.85	4.02	4.08	4.17	4.00	3.91
Genetic gain (%)	7.99	8.08	7.41	7.74	7.16	7.31	7.01	6.86

Overall, the components of genetic variance revealed that both additive and dominance type of gene actions were responsible for days to 50% tasseling in F_1 generation at CCRI, Haripur, Mansehra, and Swat. However, dominance effects were more important than additive and these F_1 hybrids could be better used in development of commercial hybrids, and the selection could also be delayed to segregating populations. In maize populations, dominant type of gene action was reported for days to 50% tasseling and other earliness traits (Sharma & Bhalla, 1990; Irshad-ul-haq *et al*., 2010; Moradi, 2014). Saleem *et al*., (2002) also concluded that days to 50% tasseling were controlled by over dominant type of gene action in different maize hybrids. For days 50% tasseling in maize, partial type of dominant gene effects were observed by Satyanarayana (1995). However, Tabassum *et al*. (2007) and Saeed and Saleem (2000) demonstrated that additive type of gene action controlled the inheritance for days to 50% tasseling in maize. Contradictions among present and past findings might be due to diverse genetic make-up of the maize breeding material and the environmental conditions where the material was studied.

Days to 50% silking: Estimation of genetic components at CCRI revealed that additive, dominance and h^2 were significant, while F and E were nonsignificant for days to 50% silking in F_1 generation (Table 4). Components showed that inheritance was inclined to nonadditive type of gene action for said trait. The F value was positive showing the abundance of dominant genes, and the same was supported by ratio of $H_1/D^{1/2}$ = 1.30. The ratio of $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (2.11) also indicated greater proportion of dominant genes. Unequal values of H_1 and H_2 and ratio of $H_2/4H_1$ (0.22) exhibited asymmetrical distribution of positive and negative genes. Significant value of h^2 revealed that dominance was unidirectional. High estimates of broad sense heritability (95%) indicated the role of dominance type of gene action for days 50% silking in F_1 generation at CCRI. Genetic gain while its value as percent of population mean were 8.08 days and 7.16%, respectively.

Under the environmental conditions of Haripur, the inheritance for days to 50% silking was appeared to be under the control of both additive and dominance type of gene actions due to significance of D, H_1, and H_2 (Table 4). Dominance components were predominant due to their greater values than additive. The covariance of additive and dominance effects (F) was positive and showing abundance of dominant genes. The ratio of dominant and recessive genes (1.58) was also greater than unity which revealed greater proportion of dominant genes and the same was also confirmed by average degree of dominance (1.50). Unequal values of H_1 and H_2 and ratio of $H_2/4H_1$ (0.23) pointed out asymmetrical distribution of positive and negative genes. Heritability in broad sense was high (0.97) and low in narrow sense (0.33) exhibiting dominance variance for days to 50% silking in F_1 generation at Haripur. Genetic gain and its value as percent of population mean were 4.17 days and 7.31%, respectively for days to 50% silking at Haripur.

Additive, dominance, F and h^2 components were significant, while E was nonsignificant for days to 50% silking in F_1 generation at Mansehra (Table 4). However, magnitude of dominance components was larger than additive and indicated importance of dominant gene action for days to 50% silking. Significant positive value of F revealed that dominant genes were more important

than recessive in parental genotypes, and the same was also narrated by ratio of dominant and recessive genes i.e., $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (2.03) showing greater proportion of the dominant genes. Significant value of h^2 (5.34) confirmed that dominance was unidirectional as supported by average degree of dominance (1.88). The ratio of $H_2/4H_1$ (0.20) and unequal values of H_1 and H_2 indicated that positive and negative genes were not in equal proportion. Broad and narrow sense heritabilities narrated that inherited genetic variation was mainly controlled by broad (93%) and less by narrow sense heritability (23%) for days to 50% silking in F_1 generation. Genetic gain while its value as percent of population mean were 4.00 days and 7.01%, respectively for days to 50% silking at Mansehra.

Components of genetic variation exhibited significant additive as well as dominance variation for days to 50% silking in F_1 generation at Swat; however, dominance components were greater than additive (Table 4). Significant positive value of F and ratio of dominant to recessive genes i.e., $4DH_1^{1/2} \pm F/ 4DH_1^{1/2} - F$ (2.07) indicated over-dominance. The dominance effects of h^2 were also supported by the ratio of average degree of dominance $H_1/D^{1/2}$ (1.45). Unequal values of H_1 and H_2 showed asymmetrical distribution of positive and negative genes in the parental inbred lines and the same was also supported by the ratio of $H_2/4H_1$ (0.22). Broad and narrow heritability values were 0.91 and 0.17 respectively for days to 50% silking in F_1 generation. Genetic gain and its value as percent of population mean were 3.91 days and 6.86%, respectively for days to 50% silking at Swat.

In four locations (CCRI, Haripur, Mansehra and Swat), both additive and dominant type of gene actions were observed for controlling the inheritance in days to 50% silking in F_1 generation. However, dominant gene action was more important than additive, therefore, the said breeding material can be used for earliness in hybrid maize. Past studies revealed non-additive type of gene action for days to 50% silking and other earliness traits in various maize populations (Saleem *et al*., 2002; Wattoo *et al*., 2009; Irshad-ul-Haq, 2010; Mousa, 2014). Guzman and Salazar (1992), Zia and Chaudhry (1980) and Kumar *et al*. (2012) also observed dominant type of gene action for days to 50% silking in maize. Contradiction in findings may be due varied genotypes and genotype by environment interactions.

Ear length: For ear length at Haripur, all the genetic components of variance were significant except environmental component in F_1 generation (Table 5). However, dominance components were found greater than additive, and nonadditive gene action controlled the inheritance for said trait. Average degree of dominance (1.21) and the ratio of $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (1.94) were greater than unity, revealed that dominant genes were in excess than recessive and displaying dominance genetic control for ear length, and the same also confirmed by positive values of F and h^2. Dominance components H_1 and H_2 values were unequal as supported by the ratio of positive and negative genes i.e., $H_2/4H_1$ (0.26) which was deviated from 0.25 in parental genotypes. Broad and narrow sense heritability estimates were observed to be 86 and 13%, respectively which revealed that majority of the genetic variation was controlled by dominant gene action for ear length in F_1 generation. Genetic gain while its values as percent of population mean were 6.74 cm and 41.05%, respectively for ear length at Haripur.

Table 5. Components of genetic variance for ear length and 1000-grain weight in 5 × 5 F_1 diallel cross of maize.

Components of genetic variance	Ear length			1000-grain weight			
	Haripur	Mansehra	Swat	CCRI	Haripur	Mansehra	Swat
D	7.42 ± 0.82*	10.40 ± 0.84*	7.26 ± 1.37*	0.001 ± 0.0003*	0.0023 ± 0.0006*	0.003 ± 0.0003*	0.005 ± 0.0003*
H_1	10.79 ± 2.23*	19.75 ± 2.27*	24.80 ± 3.71*	0.006 ± 0.001*	0.026 ± 0.0016*	0.01 ± 0.1119	0.006 ± 0.0008*
H_2	11.43 ± 2.02*	18.84 ± 2.06*	24.76 ± 3.37*	0.006 ± 0.001*	0.0269 ± 0.0014*	0.012 ± 0.0008*	0.006 ± 0.0007*
F	5.73 ± 2.06*	5.99 ± 2.10*	3.36 ± 3.43	0.001 ± 0.001	-0.0005 ± 0.0014	0.0009 ± 0.0008	0.0008 ± 0.0007
h^2	21.48 ± 1.36*	51.26 ± 1.39*	70.11 ± 2.27*	0.02 ± 0.001*	0.08 ± 0.001*	0.03 ± 0.0005*	0.02 ± 0.0005*
E	0.53 ± 0.34	0.11 ± 0.34	0.19 ± 0.56	0.0001 ± 0.0001	0.0002 ± 0.0002	0.0003 ± 0.0001*	0.0002 ± 0.0001*
$(H_1/D)^{1/2}$	1.21	1.38	1.85	2.56	3.38	2.00	1.07
$H_2/4H_1$	0.26	0.24	0.25	0.24	0.26	0.27	0.28
KD / KR	1.94	1.53	1.29	1.23	0.93	1.18	1.16
h^2/H_2	1.88	2.72	2.83	2.56	2.99	2.48	2.68
Heritability (ns)	0.13	0.36	0.24	0.16	0.13	0.10	0.51
Heritability (bs)	0.86	0.98	0.97	0.94	0.97	0.92	0.95
Genetic gain	6.74	7.68	7.61	0.18	0.19	0.18	0.19
Genetic gain (%)	41.05	46.77	46.30	59.25	61.14	57.99	59.88

Components of genetic variance showed significance of additive, dominance as well as F for ear length in F_1 generation at Mansehra (Table 5). However, dominance components were greater in magnitude and non-additive gene action control the inheritance of ear length. Average degree of dominance (1.38), positive value of F and the ratio of $4DH_1^{½} \pm F/4DH_1^{1/2} - F$ (1.53) also supported that excess of dominant genes in parental inbred lines. Significance h^2 confirms that dominance was unidirectional. H_1 and H_2 values were unequal and ratio of $H_2/4H_1$ (0.24) was deviated from 0.25, displaying unequal distribution of positive and negative genes in the parental genotypes. Broad sense heritability (98%) was higher than narrow sense heritability (36%) and revealed that majority of the genetic variation was controlled by dominant genes. Genetic gain while its value as percent of population mean were 7.68 cm and 46.77%, respectively for ear length in F_1 generation at Mansehra.

At Swat, the additive and dominance components of genetic variance were significant, while F and E were non-significant for ear length in F_1 generation (Table 5). However, the dominance components were greater than additive and the inheritance of said trait was managed by nonadditive gene action. Positive F values, and average degree of dominance $H_1/D^{1/2}$ (1.85) also revealed overdominance for ear length, and the same was also confirmed by ratio of dominant and recessive genes i.e., $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (1.29) in parental genotypes, and dominance was unidirectional due to significant h^2. Equal values of H_1 and H_2 components and ratio of $H_2/4H_1$ (0.25) indicated symmetrical distribution of positive and negative genes. High broad sense heritability estimates showed that more than 97% genetic variation was of dominance nature for ear length in F_1 generation. Genetic gain while its value as percent of population mean were 7.61 cm and 46.30%, respectively for ear length in F_1 generation at Swat.

For all the locations, the magnitude of dominance gene action was predominant and hence revealed that ear length could be deemed a vital character in selecting inbred lines for selection of superior hybrid in maize. Present results were in concurrence with findings of Hallauer and Miranda (1988) as they concluded that ear length in maize was under the control of dominance gene action. Over dominant type of gene action for genetic control of ear length in maize hybrids was also reported (Debnath & Sarkar, 1990; Chaudhary *et al*., 2000; Hadji, 2004; Ojo *et al*., 2007). However, additive genetic effects were found to be helpful in improvement of ear length in maize populations (Devi & Prodhan, 2004; Tabassum, 2004; Bujak *et al*., 2006; Asefa *et al*., 2008; Haq *et al*., 2009, 2010; Dawod *et al*., 2012 and Ali *et al*., 2014). Contradiction in findings might be due to diverse genetic make-up of the maize genotypes and the environments where studied.

1000-grain weight: Additive and dominance components of genetic variance were significant while F and E were non-significant for 1000-grain weight in F_1 generation at CCRI (Table 5). However, dominance variations were predominant, as also confirmed by average degree of dominance (2.56), F positive value, and the ratio of $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (1.23) which revealed that dominant genes were in excess than recessive. The component h^2 revealed dominance gene effects due to heterozygous loci, and the said dominance was unidirectional. H_1 and H_2 were equal and suggesting similar distribution of dominant and recessive genes, and the same was also supported by the ratio of genes with positive and negative effects i.e., $H_2/4H_1$ (0.24) which was close to 0.25. Broad sense (0.94) and narrow sense heritability (0.16) revealed that most of the genetic variation in 1000-grain weight was controlled by nonadditive genes in F_1 generation. Genetic gain and its value as percent of population mean were 0.18 kg and 59.25%, respectively for 1000-grain weight at CCRI.

Components of genetic variation showed significant values of D, H_1, H_2 and h^2, and due to greater values of dominance components, nonadditive gene action played major role in inheritance of 1000-grain weight in F_1 generation at Haripur (Table 5). Average degree of dominance i.e., $H_1/D^{1/2}$ = 3.38 was greater than unity which revealed greater proportion of dominant genes than recessive in parental inbred lines. The h^2 was significant revealing greater role of dominant genes, and the dominance was unidirectional. Equal values of H_1 and H_2 revealed that both dominant and recessive genes were equal among the parental genotypes as confirmed by ratio of $H_2/4H_1$ (0.26) which was close to 0.25, revealed same proportion of positive and negative genes. However, negative value of F and ratio of the $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (0.93) revealed greater proportion of recessive genes as compared to dominant. High estimates of broad sense heritability (0.97) and low value of narrow sense heritability (0.13) authenticated an important role of dominance gene effects for 1000-grain weight in F_1 generation. Genetic gain while its value as percent of population mean were 0.19 kg and 61.14%, respectively for 1000-grain weight in F_1 generation at Haripur. Contradiction in genetic components might be due to residual heterozygosity appeared in the parental inbred lines (Ali, 2015; Ali *et al*., 2017).

All the components of genetic variance were significant except F, however, the dominance components were greater than additive and the inheritance of 1000-grain weight was controlled by nonadditive gene action in F_1 population at Mansehra (Table 5). Significant E component also revealed some influence of environment in gene action. Average degree of dominance (2.00), F positive value and ratio of dominance to recessive genes i.e., $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (1.18) indicating greater proportion of dominant genes than recessive, and dominance was unidirectional owing to significant value of h^2. Varied distribution of dominant and recessive genes was recorded through unequal values of H_1 and H_1 and it was confirmed by ratio of unequal frequency of positive and negative i.e., $H_2/4H_1$ (0.27) which was deviated from expected value (0.25) in parental genotypes. Broad sense heritability (0.92) estimates were high as compared to narrow sense heritability (0.10) for 1000-grain weight. Genetic gain and its value as percent of population mean were 0.18 kg and 57.99%, respectively for 1000-grain weight in F_1 generation at Mansehra.

For Swat, all the genetic components were significant except F and E, and genes with additive and dominant effects were involved in inheritance of 1000-grain weight in F_1 generation at Swat (Table 5). However, dominant components were greater than additive and nonadditive gene action controlled the inheritance of this trait. Average degree of dominance i.e., $H_1/D^{1/2}$ (1.07), F positive value and ratio of dominance to recessive genes i.e., $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (1.16) revealed excess of dominant genes than recessive, and the dominance was unidirectional. Varied values of H_1 and H_2 showing asymmetrical distribution of positive and negative genes in the parental inbred lines, as supported by ratio of $H_2/4H_1$ (0.28) which was deviated from expected value (0.25). Broad sense heritability was high (0.95) while narrow sense heritability was moderate (0.51), which revealed that both dominant and additive genes were involved in inheritance of 1000-grain weight. Genetic gain and its value as percent of population mean were 0.19 kg and 59.88%, respectively for 1000-grain weight in F_1 generation at Swat.

Results revealed the involvement of genes with additive and dominance properties; however, dominance gene effects were predominant for 1000-grain weight at all the locations. Perez-Velasquez *et al*., (1996) reported dominant gene effects as major contributors to 1000-grain weight in maize populations. Additive and dominant type of gene actions were observed for inheritance of 1000-grain weight in various maize populations (Saleem *et al*., 2002; Hadji, 2004; Tabassum, 2004; Kumar *et al*., 2005; Tabassum *et al*., 2007; Hussain *et al*., 2009; Wattoo *et al*., 2009). However, additive type of gene action was found to be a major contributor in the inheritance of 1000-grain weight in maize populations (Amer*et al*., 2002; Amer, 2004; Sofi *et al*., 2006; Srdic *et al*., 2007; Moradi, 2014). Contradictions in present and previous findings might be due to diverse genetic makeup of the genotypes and the environmental effects.

Grain yield: Nonadditive gene action played an important role in expression of grain yield, as dominance components excelled the additive component for grain yield in F_1 generation at CCRI (Table 6). Overdominance for said trait was also confirmed by average degree of dominance (5.73), proportion of dominant and recessive genes in the parents i.e., $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (1.04) which were greater than unity, and F positive value exhibiting larger proportion of dominant genes than recessive in parental genotypes. Significant h^2 also confirmed that dominance was unidirectional. Values of H_1 and H_2 were not equal in magnitude and denoted unequal distribution of positive and negative genes, and the same was also supported by deviated value of $H_2/4H_1$ (0.24) from expected (0.25). Broad sense heritability was extremely high (0.99) while narrow sense was very low (0.10), which exhibited that majority of the genetic variation was caused by dominance genes for grain yield. Estimate of genetic gain for grain yield was 7606.51 kg ha^{-1}, while its value as percent of population mean was 84.02% grain yield in F_1 generation at CCRI.

Table 6. Components of genetic variance for grain yield in 5 × 5 F_1 diallel cross of maize.

Components of genetic variance	Grain yield			
	CCRI	Haripur	Mansehra	Swat
D	361446.66 ± 489126.47	2308504.60 ± 382130.26*	838927.41 ± 2023070.52	1996575.73 ± 420907.86*
H_1	11883582.98 ± 1320943.37*	19580254.57 ± 1031987.57*	32035014.49 ± 5463539.07*	28112020.82 ± 1136711.01*
H_2	11636444.67 ± 1198110.28*	19540715.08 ± 936024.16*	30533199.18 ± 4955490.48*	28526075.16 ± 1031009.49*
F	83914.78 ± 1221837.54	1207332.77 ± 954561.09	611497.06 ± 5053628.54	477111.73 ± 1051427.50
h^2	32333400.32 ± 808899.45*	57461356.99 ± 631953.04*	85944237.98 ± 3345679.95*	84402712.10 ± 696082.01*
E	30981.86 ± 199685.05	44527.32 ± 156004.03	80948.60 ± 825915.08	113954.39 ± 171834.91
$(H_1/D)^{1/2}$	5.73	2.91	6.18	3.75
$H_2/4H_1$	0.24	0.25	0.24	0.25
KD / KR	1.04	1.20	1.13	1.07
h^2/H_2	2.78	2.94	2.81	2.96
Heritability (ns)	0.10	0.11	0.10	0.07
Heritability (bs)	0.99	0.99	0.99	0.98
Genetic gain	7606.51	7606.51	7606.51	7529.68
Genetic gain (%)	84.02	84.02	84.02	83.18

Additive and dominance components (D, H_1, H_2, h^2) were found to be significant and both additive and nonadditive components were involved in inheritance of grain yield in F_1 generation at Haripur (Table 6). Dominance genetic variances played an important role in expression of above trait due to their higher values. Average degree of dominance i.e., $H_1/D^{1/2}$ (2.91) and proportion of dominant and recessive genes in the parents (1.20) were greater than unity, and positive F value, revealed greater proportion of dominant genes than recessive in the parental inbred lines. The component h^2 was significant, showing the presence of dominance gene effects due to heterozygosity at many loci. Comparable values of H_1 and H_2 showed symmetrical proportion of positive and negative genes frequencies, and the same was also authenticated by ratio of $H_2/4H_1$ (0.25). High estimates of broad (0.99) and low narrow (0.11) sense heritabilities were observed which indicated major role of dominant gene action for grain yield. Estimate of genetic gain was 7606.51 kg ha^{-1}, while its value as percent of population mean was 84.02% in F_1 generation at Haripur.

Components of dominant genetic variance (H_1, H_2, h^2) were important in expression of grain yield, because dominance components excelled the additive component in F_1 generation at Mansehra (Table 6). Positive value of F exhibited that dominant genes prevailed over recessive genes as substantiated by the ratio of dominant to recessive genes i.e., $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (1.13) and mean degree of dominance i.e., $H_1/D^{1/2}$ (6.18) which were greater than unity and revealed overdominance. Varied values of H_1 and H_2 revealed the presence of unequal frequencies of positive and negative genes which also confirmed by the ratio of $H_2/4H_1$ (0.24) on its deviation from the expected value (0.25). Heritability in narrow sense (0.10) was least while broad sense heritability (0.99) was higher for grain yield. Heritability revealed that greater portion of inherited genetic variation was of dominance nature. For grain yield, genetic gain was 7606.51 kg ha^{-1}, while its value as percent of population mean was 84.02% for grain yield in F_1 generation at Mansehra.

Components of genetic variance revealed that additive and dominance components (H_1, H_2, h^2) were significant and both were involved in inheritance of grain yield in F_1 generation at Swat (Table 6). Dominance genetic variances played an important role in expression of said trait due to their higher values. Average degree of dominance (3.75) and ratio of $4DH_1^{1/2} \pm F/4DH_1^{1/2} - F$ (1.07) in the parental genotypes were greater than unity, and positive value of F also exhibited greater proportion of dominant genes than recessive in the parental inbred lines. The dominance was unidirectional due to significant h^2, revealing dominance effects due to heterozygosity at loci. Comparable values of H_1 and H_2 showed symmetrical distribution of positive and negative genes as confirmed by non-deviated ratio of $H_2/4H_1$ (0.25). High estimates of broad sense heritability (0.98) indicated major role of dominant gene action for inheritance of grain yield. Estimation of genetic gain was 7529.68 kg ha^{-1}, while its value as percent of population mean was 83.18% for grain yield in F_1 populations at Swat.

At Haripur and Swat both dominance and additive components while at CCRI and Mansehra only nonadditive gene effects were involved in expression of grain yield in F_1 generation. Overall, nonadditive gene action was found responsible for genetic variation and inheritance of grain yield at all the locations. In past studies, dominant gene effects were found to be responsible for inheritance of grain yield in various maize populations (Unay *et al*., 2004; Wardyn *et al*., 2007; Dawod *et al*., 2012; Kumar *et al*., 2012; Agrawal *et al*., 2014; Moradi, 2014; Soni & Khanorkar, 2014). Present results were also in corroboration with findings of Srdic *et al*. (2007), Wattoo *et al*. (2009), Zare *et al*. (2011a, b) and Hussain *et al*. (2014) as they observed overdominance type of gene action for grain yield in different maize hybrids. However, additive type of gene action was observed in some earlier studies for inheritance of grain yield in maize populations (Ojo *et al*., 2007; Hussain *et al*., 2009; Chohan *et al*., 2012; Mousa, 2014). Important role of both additive and nonadditive gene effects in inheritance of maize grain yield was recorded by Giridharan *et al*. (1996), Zehui *et al*. (2002) and Kumar *et al*. (2006). Contradiction in present and past findings might be due to varied genetic makeup of maize populations and genotype by environment interaction.

Conclusion

Additive-dominance model was adequate/partially adequate for various traits at all the locations. Dominance components were predominant and overdominance type of gene action played an important role in inheritance of earliness and yield traits in maize at all the locations. Broad sense heritability values were high while narrow sense heritability values were low to moderate. Due to nonadditive genes control of various traits and high broad sense heritability, the promising F_1 hybrids can be used in future breeding programs for production of early maturing/high yielding maize hybrids, and cultivars through later segregating generations.

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